

**CHEMICAL AND BEHAVIORAL DEFENSES OF A
NEOTROPICAL CAVERNICOLOUS HARVESTMAN:
GONIOSOMA SPELAEUM
(OPILIONES, LANIATORES, GONYLEPTIDAE)**

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ABSTRACT. *Goniosoma spelaeum* (Mello-Leitão 1932), a cavernicolous species in the Ribeira Valley, southeastern Brazil, was studied in the field and laboratory. The defensive behaviors were: nipping with the chelicerae; delivery of a sharp pinch with the fourth coxae and femora; rapidly running away; dropping from the cave ceiling and remaining concealed against the substrate; and emission of a chemical defense compound. The delivery mechanisms of the defensive secretion were either by spreading the substance on its own body through a lateral groove, or by projecting it as a jet directly at the aggressor. The defensive substance is a mixture of enteric fluid, which runs from the mouth into ventral and lateral channels, with quinones collected from the scent gland openings located next to the lateral margins of coxae II. Electron microscope analysis of the external structure of the exocrine gland opening revealed a second aperture which could be responsible for the jet emission. Two quinones (2-ethyl-1,4-benzoquinone and 2,3,5-trimethyl-1,4-benzoquinone) were identified from the defensive secretion; the first is reported herein for the first time in opilionids. Four other species of *Goniosoma* Perty 1833 from epigean and hypogean environments showed similar behaviors.

Studies on the defensive behavior of harvestmen are relatively few, and most deal with species of suborder Palpatores from the Northern Hemisphere. In this group, autotomy of legs is suggested as the most important defensive behavior (Berland 1949; Edgar 1971; Kaestner 1968). Also common in Palpatores is the shaking of the body (Berland 1949) and the presence of bright white bands on the distal portions of two or more legs (J. Cokendolpher pers. comm.), which probably hinders the identification and exact location of the harvestman's body.

Some harvestmen feign death and become rigid (Cokendolpher 1987; Eisner et al. 1971). Long-legged species run away rapidly (Bristowe 1925; Edgar 1971). Others drop to the ground, where they stay motionless and concealed amongst the substrate, thus confounding their predators (Duffield et al. 1981; Edgar 1971; Hillyard & Sankey 1989). Some Gonyleptidae (suborder Laniatores), when taken in hand, flex their fourth legs quickly toward

the body in order to deliver a sharp pinch to the aggressor between the armature of both the coxae and femora. This has been reported for *Goniosoma longipes* (Roewer 1913) and *G. roridum* Perty 1833 from Ouro Preto, Brazil (Bristowe 1925) and *Acanthopachylus aculeatus* (Kirby 1819) from Uruguay (Capocasa & Bruno-Trezza 1964).

However, the best known defensive behavior, which is considered most effective in Laniatores and Cyphophthalmi, is chemical exudation (see review in Eisner et al. 1978). The animals secrete chemical substances from a pair of exocrine glands ("scent glands") which open on the cephalothorax next to the lateral margins of coxae I in Palpatores, or coxae II in Laniatores and between coxae II and III in Cyphophthalmi (Juberthie 1961, 1976). The mechanisms of delivery of the defensive secretion in harvestmen are diverse, as summarized by Acosta et al. (1993).

Chemical analyses of defensive exudates have shown that, among the Laniatores, the

Gonyleptoidea produce a variety of alkylated benzoquinones and phenols (Eisner et al. 1971, 1977; Estable et al. 1955; Fieser & Ardao 1956; Roach et al. 1980), and the Travunioidea produce mainly terpenoids (Ekpa et al. 1984). In contrast, among the Palpatores, the Leiobuninae secrete short-chain acyclic ketones and alcohols (Blum & Edgar 1971; Ekpa et al. 1985; Jones et al. 1976, 1977; Meinwald et al. 1971), whereas the Phalangiinae produce naphthoquinones, which were considered to be rare as natural products (Wiemer et al. 1978). No chemical data are available for species of Cyphophthalmi, but the orangish coloration of the gland contents in at least one *Siro* species may suggest the presence of a quinone (J. Cokendolpher pers. comm.).

Studies on the chemistry of exocrine secretions of harvestmen have been restricted to species from the Northern Hemisphere, with two exceptions: *Acanthopachylus aculeatus* from Uruguay (Estable et al. 1955; Fieser & Ardao 1956) and *Pachyloidellus goliath* Acosta 1993 from Argentina (Acosta et al. 1993). Furthermore, all species studied dwell in epigeal environments.

This paper is part of a general natural history study of cavernicolous harvestmen, conducted from November 1991 to August 1993 in the Ribeira Valley, southeastern Brazil (see Gnaspini 1995, 1996). In the present study, we report on the defense of *Goniosoma spelaeum* (Mello-Leitão 1932) (Laniatores, Gonyleptidae, Goniosomatinae), a cavernicolous species in the Ribeira Valley, São Paulo state, southeastern Brazil. Observations on other *Goniosoma* species (*G. proximum* (Mello-Leitão 1922), *G. varium* Perty 1833 and two undescribed species near *G. badium* C.L. Koch 1839) were made occasionally.

METHODS

The harvestmen studied were either observed in the field or in an underground laboratory in São Paulo, with environmental conditions similar to those of the caves in which they were captured. Behavioral analysis was conducted both while handling the specimens and later, based on video tapes taken during handling.

Goniosoma spelaeum is a large harvestman—the adults have a body about 1 cm long and 1 cm wide, and often reach more than 20 cm in diameter with the legs spread. They are

very common and widely distributed in caves throughout the Ribeira Valley, in São Paulo state (see Gnaspini 1995, 1996).

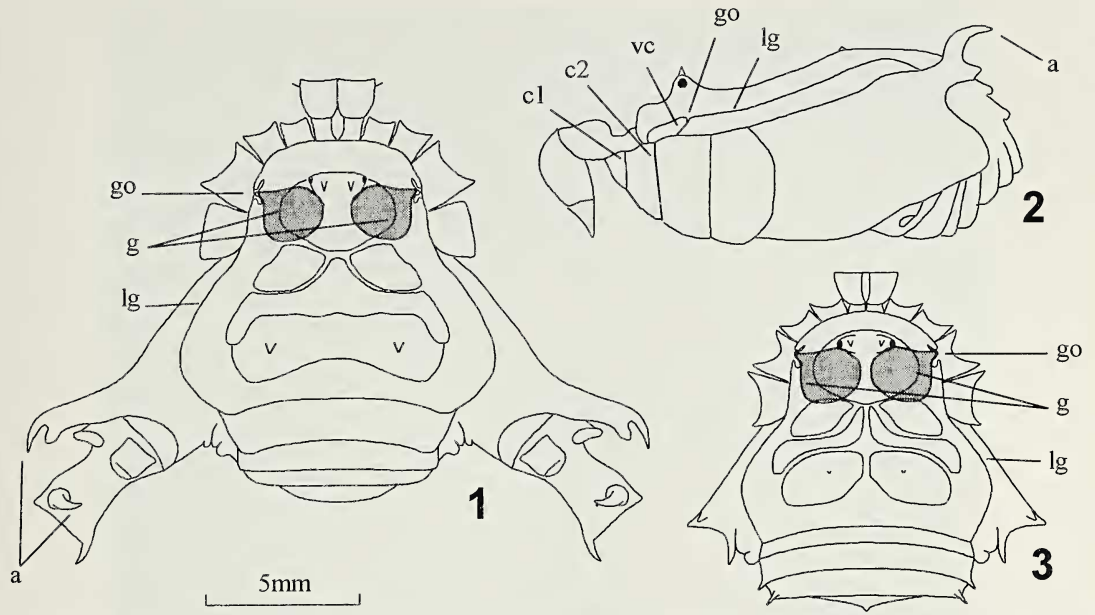
During the field study, more than 2000 individuals of *G. spelaeum* (adults and juveniles) were captured, handled and marked (in order to allow individual recognition for another study). Defensive behavior was elicited and observed on most of those specimens. Observations on *G. proximum*, *G. varium* and two undescribed species (related to *G. badium*) were made occasionally. Besides handling the animals, defensive behavior could also be induced by shining a light on them or by approaching them. Emission of chemical secretion of *G. spelaeum* was also observed under a stereomicroscope in the laboratory.

Defensive secretions were collected in the laboratory directly from 10 live specimens of *G. spelaeum* after its release. This secretion was diluted by the animals with oral fluids, as is common in other harvestmen studied (e.g., Eisner et al. 1971). To obtain concentrated samples, five freshly killed specimens were dissected and the glandular contents were aspirated into glass tubes. Chemical analyses were made with a Varian 2400 gas chromatograph using a capillary column DB-5 coupled with a Finnigan MAT ITDS80 mass spectrometer. The substances were identified by comparing their mass spectra with those published by McLafferty & Stauffer (1989). The external morphology of the gland opening was studied under a Zeiss DSM 940 scanning electron microscope.

A series of *G. spelaeum* vouchers was deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

RESULTS

The defensive behaviors observed in *Goniosoma spelaeum* included nipping with the chelicerae, delivery of a sharp pinch with the fourth coxae and femora, rapid running away, dropping from the cave ceiling, and emission of a chemical defense compound. The defensive substance is a mixture of enteric fluid, which runs from the mouth into ventral and lateral channels, with quinones collected from the gland opening located next to coxa II. The delivery mechanisms of the defensive secretion were either by spreading the substance on its own body through a lateral groove, or by projecting it as a jet directly at the aggressor.



Figures 1–3.—*Goniosoma spelaeum*, habitus of adult male and female, showing defense features. 1, Dorsal view, male; 2, Lateral view, male; 3, Dorsal view, female. *a* = armature of coxa and trochanter; *c1* = channel between coxae of pedipalp and leg I; *c2* = channel between coxae of legs I and II; *g* = glands (hatching); *go* = gland opening; *lg* = lateral groove; *vc* = vertical channel connecting *c1* and *c2* with *lg*.

Gland opening and fluid displacement.—All *Goniosoma spelaeum* harvestmen have one pair of internal glands which open dorso-laterally over coxae II (Figs. 1–3). The discharge of these glands generally mixes with enteric fluid, as will be discussed in the next section. The enteric fluid, coming from the mouth, reaches the gland openings by capillarity through a sequence of channels (as in Figs. 1–3). First, there are two pairs of ventral channels—one is located between the coxae of the pedipalps and legs I (*c1* of Fig. 2); the other lies between the coxae of legs I and II (*c2*), and its white color sharply contrasts with the yellowish coxae. Observations with a stereomicroscope revealed that flow through channel *c2* seems to be more common than through *c1*; however, the position in which the specimen is placed for examination may influence the direction the fluid travels. Independently, these ventral channels reach a horizontal lateral channel defined within the soft pleura between the dorsal scutum and the coxae insertions. Finally, just in front of the gland opening, there is a vertical channel (*vc*, which is actually somewhat oblique), which connects the lateral channel with the lateral groove (*lg*).

In some cases the fluid may run by capillarity through the lateral groove, collecting posteriorly on coxae IV, as will be discussed later.

Whereas there is a single gland opening in other opilionids (e.g., Juberthie 1961, 1976), in *G. spelaeum* the structure of the gland opening region is more complex (Fig. 4). In addition to the actual gland opening located at the lateral margin of the scutum (*go* of Fig. 4), there are two secondary outlets located dorso-laterally and connected to “*go*” by very short channels: one anterior (*a* notch, *ga*), and one posterior (*gp*, with its internal integument covered with several small sharp projections, as in Fig. 5). Probably, after being released by the actual opening (*go*), the secretion runs anteriorly to *ga* or posteriorly to *gp*. Unfortunately, release through these openings was not observed through a microscope, and this hypothesis is based on the morphology of the region and on observations of the path taken by the fluid running nearby, and deserves further investigation. Actually, the running fluid bathes the posterior opening when coming from the lateral channel towards the lateral groove. Observations made with a microscope



Figure 4.—*Goniosoma spelaeum*, dorsal view of left lateral margin, showing region of gland opening. *ac*, *ac*⁺ = dorsal apophyses of coxa II; *dt* = tubercle dorsal to the gland opening; *ga* = anterior gland outlet (notch); *go* = gland opening; *gp* = posterior gland outlet; *lg* = lateral groove; *sp* = sensitive peg; *vc* = vertical channel which connects channels between coxae coming from the mouth with the lateral groove just in front the gland opening. Scale = 200 μ m.

did not clearly reveal if this bath occurs over or through the posterior opening.

Besides a large dorsal apophysis on coxae I and II, as on *Pachyloidellus goliath* (Acosta et al. 1993), *G. spelaeum* has three small dorso-lateral apophyses on coxae II directed towards the gland opening (*ac*, Fig. 4). The larger anterior apophysis (*ac*⁺) is placed exactly over the position where the ventral channel *c2* meets the lateral channel.

The lateral groove, into which the defensive substance is released by the gland opening, is smooth and very shallow in *G. spelaeum* and has several pegs (probably sensory, as their shape is similar to sensorial pegs of other arthropods) along its margin (Fig. 4). The exact function of these pegs has not been studied. The defensive fluid bathes these pegs as it runs

along the groove. The lateral groove starts slightly anterior to the gland opening and defines a continuous passage for the fluid coming from the ventral channels via the vertical channel and the lateral groove (Fig. 4). Thus, the secretion from the gland is released directly into the running enteric fluid from the mouth.

Chemical defensive behavior.—In the following discussion we use the codes for the mechanisms of delivery as proposed and listed by Acosta et al. (1993). Besides creating a “chemical shield” around their bodies, harvestmen may squirt the exudate as a jet or administer it by dabbing with the legs onto an aggressor. All species of *Goniosoma* considered in this study showed two of these behaviors: chemical shield and squirting. However,



Figure 5.—*Goniosoma spelaeum*, dorsal view of right lateral margin. Detail of the posterior gland outlet, showing internal integument which is covered with sharp projections. *gp* = posterior gland outlet; *ii* = internal integument; *lg* = lateral groove; *sp* = sensorial peg. Scale = 20 μ m.

we did not find a preference for one or the other delivery mechanism—the same specimen would either emit a jet or form a shield during subsequent handling. Leg dabbing was not observed.

In the *G. spelaeum* mechanism of “displacement of the liquid along the lateral area of the scutum” (coded as 2.2. by Acosta et al. 1993), the enteric fluid passes in front of the opening, where it may collect some secretion, and runs through the lateral groove down to coxae IV, where it forms a droplet (as in Figs. 6, 7). It should be noted that the mixing may not occur. Sometimes, the coxal droplet contains only enteric fluid, as indicated by its lack of smell and clear color, as in Fig. 6. This droplet may stay clear, i.e., the animal may not release secretion into it. This probably occurs when there is no secretion left in the gland or when the animal does not consider

releasing it. Secondly, the secretion can be released after the droplet is formed. In this case, the clear droplet (as in Fig. 6) becomes turbid and yellowish (as in Fig. 7). Thirdly, the secretion can be released while the enteric fluid is running in front of the gland opening. In this case, the droplet which is formed, as well as the fluid over the lateral groove, is already turbid and yellowish (also as in Fig. 7). Therefore, the same final aspect (turbid droplet) may take one or two steps to be achieved. Then, this droplet is retained on the coxae IV, where it evaporates. The formation of droplets, always on coxae IV, is not a normal condition of the species, occurring only after handling, and it is thus probably a defensive behavior.

Another common defensive behavior of *G. spelaeum* was the “emission in form of a fine jet upwards and backwards” (coded as 3.1. by



Figure 6.—*Goniosoma spelaeum*, dorsal view, showing two droplets (arrows) formed only by enteric fluid, which is clear. Scale = 10 mm.

Acosta et al. 1993). In *G. spelaeum*, the jet is emitted directly from the gland opening and extends at least 5 cm, and very often 10 cm or more. It can be emitted in any direction, even forward. Whichever was the region of the animal body handled, the jet emitted usually reached the observer's hands. This jet is

bright yellow and becomes reddish after a few seconds. When seized by the fourth pair of legs, *G. spelaeum* may also turn its body quickly backwards while emitting the jet, probably enhancing the chance of the substance hitting and spreading upon the aggressor.



Figure 7.—*Goniosoma spelaeum*, lateral view, showing the turbid droplet of secretion (arrow) formed by the mixture of enteric fluid and defensive exudate. Scale = 10 mm.

Chemical analysis of the defensive exudate.—The odor and yellowish color of the defensive exudate of *Goniosoma spelaeum*, combined with the fact that it stained human skin with a reddish spot, suggested that it might contain one or more quinones. Laboratory analyses confirmed the mixture of benzoquinones in *G. spelaeum* secretion. Gas chromatography and mass spectrometry analyses of secretion taken directly from the glands showed the presence of two components. The major component (ratio about 7:3), which had a molecular ion m/z of 136, was identified as 2-ethyl-1,4-benzoquinone. The other component, a molecular ion m/z of 150, was identified as 2,3,5-trimethyl-1,4-benzoquinone. Moreover, analysis of the mixture taken from live animals detected only water in addition to the two quinones. This means that the enteric fluid contained only water. Therefore, the defensive exudate contains two quinones from the gland mixed with water from the enteric fluid.

Other behavioral defenses.—Individual *Goniosoma* did not shake their body, autotomize their legs, or feign death when handled. If disturbed, *G. spelaeum* tried to escape by running fast and also frequently by dropping from the cave ceiling and remaining motionless for a while to avoid detection. Later they would crawl up the cave walls. The mere approach of an observer often caused the animals to drop. In addition, as already reported for other *Goniosoma* (Bristowe 1925), *G. spelaeum* try to deliver a nip to the offending object by pinching it between their fourth coxae and femora (which seems to be more effective among males because they are more highly armed than females—see Figs. 1–3), sometimes painfully. They always reacted with this behavior when handled near the fourth leg coxae/trochanter articulation. When handled near the oral region, *G. spelaeum* always seized an observer's fingers with its pedipalps and tried to bite with its chelicerae, always harmlessly.

DISCUSSION

External morphology, fluid displacement, and chemical defensive behavior.—The scent glands of *Goniosoma spelaeum* open over coxae II, and are connected by arrangements of channels to the mouth as in other Laniatores (e.g., Eisner et al. 1971; Acosta et

al. 1993). The arrangement in *G. spelaeum* is very similar to that of *Pachyloidellus goliath* (as in figs. 1–3 of Acosta et al. 1993). Although the dorsal apophyses on coxae I and II were considered not to be involved in liquid displacement in *P. goliath* (Acosta et al. 1993), the apophyses on coxae II of *G. spelaeum* are directed towards the gland opening and the larger apophysis (ac^+ of Fig. 4) is placed exactly over the position where ventral channel $c2$ meets the lateral channel. Therefore, it might serve to avoid the overflow of fluid at this sharp turning point. The role of these apophyses in liquid displacement remains to be tested. However, the volume of running fluid is sometimes large and the apophyses might be serving to regulate the upper level preventing overflow.

In the mechanisms of “displacement of the liquid along the lateral area of the scutum” (coded as 2.2. by Acosta et al. 1993) and of “emission of a secretion globule on the gland opening, that is directed to the aggressor with the forelegs” (coded as 3.2.), the chemical substance released by the gland openings may be mixed with oral fluid (basically water, as stated by Eisner et al. 1971) which runs by capillarity in grooves between the anterior coxae to reach the gland opening. Besides our record herein, it has been shown to occur only in *Pachyloidellus goliath* (Acosta et al. 1993), and in all Cosmetidae studied by Eisner et al. (1971, 1977). We should stress that both mechanisms have common steps: first, the enteric fluid from the mouth collects in front of the gland opening; then the secretion is discharged from the gland. At this point, a droplet of mixed fluids is formed in front of the gland opening (which resembles the mechanism of “emission of a secretion globule at the gland opening”, coded 1.2., common in some Palpatores and in some Laniatores as well). Afterwards, this droplet may follow the lateral groove as in mechanism 2.2. in *P. goliath*, or be administered by leg dabbing as in mechanism 3.2. in Cosmetidae. Another case with similar (but not all) steps was reported for *Zygopachylus albomarginis* Chamberlin 1925 (Cokendolpher 1987). Although *Z. albomarginis* is listed under the same code 2.2. of Acosta et al. (1993), this species shows two differences from above: the liquid is displaced along a row of tubercles (and not along a lateral groove, as noted by Acosta et al. 1993);

and no droplet is formed in front of the opening; i.e., the secretion oozes from the pore and runs along the lateral margin, and the fluid is then collected distally on a spine forming a droplet (Cokendolpher 1987). This difference in timing of droplet formation was not included in the table from Acosta et al. (1993). In *Goniosoma spelaenum*, a further variation is here registered: the droplet will also be formed distally (always on coxae IV), and not in front of the opening (like in *Z. albomarginis*), but runs through a lateral groove (like in *P. goliath*).

Mixing of glandular secretion with enteric fluid, and its displacement in grooves along the scutum area was reported by Acosta et al. (1993) to be common in Gonyleptidae; at least for Pachylinae, from which several species were morphologically analyzed. In some Gonyleptinae studied, those authors did not find well-defined grooves on the lateral area as they did in Pachylinae. Herein, we noticed the channels pattern in Pachylinae (mouth to gland opening, and towards the body posterior end) also seems to be the rule in Goniosomatinae. However, in the latter the main difference is that there is no droplet formation in front of the gland opening and subsequent running through the groove; i.e., in *Goniosoma* species, the droplet is only formed distally on coxae IV. Moreover, the droplet may or may not contain secretion; and, when it does, the mixture may take place while the enteric fluid runs in front of the opening, or afterwards, when the droplet is already formed. As far as we know, these different timings of mixture were not reported before in harvestmen.

The "emission in form of a fine jet upwards and backwards" (coded as 3.1. by Acosta et al. 1993), which in *G. spelaenum* takes place directly from the gland opening and extends several centimeters in any direction, even forward, has been reported previously only in Triaenonychidae (Lawrence 1938; Maury 1987). However some striking differences were observed. In *Triaenonychoides* spp. the jet might squirt up to 1 cm in distance (Maury 1987) and in *Larifuga capensis* Lawrence 1931 and *Larifugella natalensis* (Lawrence 1931) it extends at least 2.5 cm (Lawrence 1938). In the Triaenonychidae the jet can be emitted only upwards and backwards (Lawrence 1938). However, this author stated that

it might have been due to fixing the animals in such a position that they could not direct the jet, and that it is probable that the animal has some control over the direction in which ejection takes place.

Morphologically, *G. spelaenum* also has secondary outlets at the gland opening region (*ga* and *gp* of Fig. 4). These outlets are probably related to fluid displacement immediately after release from the gland opening, although their function is still not clear. Although, there also seems to be a second opening in *P. goliath* (as in figs. 2, 3 of Acosta et al. 1993), unfortunately those authors did not cite nor comment on it.

Because both the second posterior gland outlet and the powerful jet emitting behavior are first reported herein, we supposed they might be related with each other. Thus, somehow the second opening with its sharp internal projections may be related to the ability of extended jet emission; however, it remains to be tested. Unfortunately, no jet was emitted while studying live animals under a microscope. Therefore, it was not possible to determine the path taken by the secretion. Moreover, when analyzing the illustration of the gland opening in *L. natalensis* (fig. 2b in Lawrence 1938), which also emits a jet, there seem to be two outlets, one anterior and one posterior. Thus, external morphology of the gland opening of jet emitting harvestmen needs further detailed study.

Chemical analysis of exudate.—Fieser & Ardao (1956) stated that, among benzoquinones, some typically show a characteristic yellow color: 2,3-dimethyl-1,4-quinone, 2,5-dimethyl-1,4-quinone, 2,6-dimethyl-1,4-quinone, and 2-ethyl-1,4-quinone. As can be seen in the summary from Acosta et al. (1993), the first is the most common secretion recorded from gonyleptoid harvestmen; the second was detected in two species; and the second most common gonyleptoid compound is 2,3,5-trimethyl-1,4-quinone.

Laboratory analyses of the yellowish chemical exudate of *Goniosoma spelaenum* identified 2-ethyl-1,4-quinone (the fourth in Fieser & Ardao's list given above) as the major component, and 2,3,5-trimethyl-1,4-quinone as the second component. The major compound is here reported for the first time for opilionids. The second is common in several of the Gonyleptidae and Cosmetidae (Laniatores) studied

(see Acosta et al. 1993). It is noteworthy that the latter was never the major component in secretions of the harvestmen from which it was identified (e.g., Eisner et al. 1977).

Other behavioral defenses.—The *Goniosoma spelaum* behavior of dropping from the ceiling and remaining motionless for a while probably evolved as a defense against epigean predators and has been maintained because these harvestmen inhabit the twilight zone and leave the caves for feeding. This does not constitute feigning death because, if taken from the floor and handled, they tried to escape. The behavior of delivering a nip to the offending object by pinching it between their fourth coxae and femora was also reported for *Acanthopachylus aculeatus*, by Capocasale and Bruno-Trezza (1964), who stated that one is led to release the animals because of the shock, not because this behavior could harm the observer. In contrast, we found that the very sharp armature of *G. spelaum* was painful, and sometimes caused bleeding. Finally, the common behavior of biting with the chelicerae, although harmless to human skin, may be effective with smaller aggressors.

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